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Abstract: Chimpanzees are renowned for their use of foraging tools in harvesting social insects and some populations use tools to prey on aggressive army ants (Dorylus spp.). Tool use in army ant predation varies across chimpanzee study sites with differences in tool length, harvesting technique, and army ant species targeted. However, surprisingly little is known about the detailed ecology of army ant predation. We studied army ant predation by chimpanzees (Pan troglodytes verus) at the Seringbara study site in the Nimba Mountains, Guinea (West Africa), over 10 years (2003-2013). We investigated chimpanzee selectivity with regards to army ant prey species. We assessed the temporal variation in army ant-feeding and examined whether army ant predation was related to rainfall or ripe fruit availability. Moreover, we examined whether chimpanzees showed selectivity regarding plant species used for tool manufacture, as well as the relationship between tool species preference and tool collection distance. Lastly, we measured tool properties and investigated the use of tool sets and composite tools in army ant predation. Seringbara chimpanzees preyed on one army ant species (D. nigricans) more often than expected based on encounter rates, which may be explained by the overlap in altitudinal distribution between chimpanzees and D. nigricans. Army ant predation was not related to rainfall or fruit availability. Chimpanzees were selective in their choice of tool materials and collected their preferred tool species (Alchornea hirtella) from greater distances than they did other species. Lastly, Seringbara chimpanzees used both tool sets and composite tools (tree perch) in army ant predation. Tool types (dig vs. dip) differed in width and strength, but not length. Tool composites were found at 40% of ant-feeding sites. Our study sheds new light on the ecology of army ant predation and provides novel insights into chimpanzee selection of army ant prey and tool species.

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Chimpanzees Prey on Army Ants at Seringbara, Nimba Mountains, Guinea: Predation Patterns and Tool Use Characteristics

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ABSTRACT

Chimpanzees are renowned for their use of foraging tools in harvesting social insects and some populations use tools to prey on aggressive army ants (*Dorylus* spp.). Tool use in army ant predation varies across chimpanzee study sites with differences in tool length, harvesting technique, and army ant species targeted. However, surprisingly little is known about the detailed ecology of army ant predation. We studied army ant predation by chimpanzees (*Pan troglodytes verus*) at the Seringbara study site in the Nimba Mountains, Guinea (West Africa), over 10 years (2003-2013). We investigated chimpanzee selectivity with regards to army ant prey species. We assessed the temporal variation in army ant-feeding and examined whether army ant predation was related to rainfall or ripe fruit availability. Moreover, we examined whether chimpanzees showed selectivity regarding plant species used for tool manufacture, as well as the relationship between tool species preference and tool collection distance. Lastly, we measured tool properties and investigated the use of tool sets and composite tools in army ant predation. Seringbara chimpanzees preyed on one army ant species (*D. nigricans*) more often than expected based on encounter rates, which may be explained by the overlap in altitudinal distribution between chimpanzees and *D. nigricans*. Army ant predation was not related to rainfall or fruit availability. Chimpanzees were selective in their choice of tool materials and collected their preferred tool species (*Alchornea hirtella*) from greater distances than they did other species. Lastly, Seringbara chimpanzees used both tool sets and composite tools (tree perch) in army ant predation. Tool types (dig vs. dip) differed in width and strength, but not length. Tool composites were found at 40% of ant-feeding sites. Our study sheds new light on the ecology of army ant predation and provides novel insights into chimpanzee selection of army ant prey and tool species.

Keywords: insectivory; tool use; army ants; chimpanzee; ant dip

INTRODUCTION

Insects are eaten by a wide variety of primate species, ranging from prosimians to great apes [McGrew, 2001; McGrew, 2014]. Among the African apes, chimpanzees are renowned for using different types of tools to feed on social insects, including termites (Termitidae) and ants (Formicidae). Social insects provide a concentrated and sizeable food source, but they also have defense strategies, such as painful bites and formidable mounds. By using extractive foraging tools, chimpanzees are able to access these prized food sources less painfully and to increase their feeding efficiency and caloric intake [McGrew, 1992]. A well-studied type of extractive insect foraging is ant-dipping to prey upon army (or driver) ants in the subgenus *Dorylus* (*Anomma*) [McGrew, 1974]. In ant-dipping, chimpanzees use a stiff 'wand' of woody or herbaceous vegetation to extract the highly aggressive army ants from their temporary underground nests [McGrew, 1974] or directly from surface trails [Sugiyama, 1995; Humle & Matsuzawa, 2002]. Army ants are ubiquitous across chimpanzee study sites, and tool use in army ant predation has been recorded in more than a dozen chimpanzee populations [see review in: Schöning et al., 2008a].

Army ant predation by chimpanzees shows considerable variation across study sites [Schöning et al., 2008a]. Whereas some chimpanzee communities feed predominantly on brood and eggs dug by hand from the nest, others focus on ant-dipping [Möbius et al., 2008]. Tool use in army ant predation also varies across sites with differences in tool length, harvesting technique, context (nest vs. trail) and army ant species targeted. A detailed study on ant-dipping behavior at Bossou, Guinea, showed an effect of prey characteristics on tool length (i.e. longer tools for more

aggressive ants) and dipping technique, thereby highlighting how the prey species shapes the predator's behavior [Humle & Matsuzawa, 2002].

However, little is known about the detailed ecology of chimpanzee predation on army ants. Specifically, chimpanzee selectivity with regard to prey species of army ants has remained unstudied. To assess whether or not chimpanzees selectively eat certain army ant species, we need to know army ant species availability and chimpanzee predation patterns. Additionally, chimpanzee tool selectivity with regards to plant species has yet to be systematically tested. Tool-material selectivity in ant-dipping has been reported for chimpanzees at Goualougo, Republic of Congo [Sanz & Morgan, 2007], but information on tool material availability was not assessed. Generally, chimpanzees seem to collect tools for ant-dipping within arm's reach of the nest [McGrew, 1974; Boesch & Boesch, 1990; Sugiyama, 1995; Hashimoto et al., 2002; Sanz & Morgan, 2007; Sanz et al., 2010; Pascual-Garrido et al., 2012], but no data are currently available on the potential preference for certain plant species as raw material.

Chimpanzees at Goualougo use 'tool sets' in army ant predation, involving perforating and dipping tools [Sanz et al., 2010]. Tool sets are defined as the obligate sequence of two or more types of tools used to achieve a single goal [Brewer & McGrew, 1990; McGrew, 2013]. Tool sets have been reported at several chimpanzee study sites for termite-fishing (e.g. Republic of Congo: Sanz et al. 2004; Cameroon: Deblauwe et al. 2006; Gabon: McGrew and Rogers 1983) and honey-gathering (e.g. Republic of Congo: Sanz and Morgan 2009; Gabon: Boesch et al. 2009; Central African Republic: Hicks et al. 2005), but ant-dipping tool sets are observed rarely [Bossou, Guinea: Sugiyama, 1995; Seringbara, Guinea: Humle & Matsuzawa, 2001; Goualougo, Republic of Congo: Sanz et al., 2010]. In addition to tool sets, chimpanzees use 'tool composites' in army ant predation [McGrew, 1974; McGrew, 2013]. Tool composites

101 are defined as two or more types of tools used simultaneously and complementarily to
102 achieve a goal. In army ant predation, this entails the use of a tree sapling to make an
103 elevated perch from which to dip more securely for biting army ants on the ground
104 below [McGrew, 1974]. A tree perch can be considered a tool in that it comprises a
105 'manipulable attached' object [Shumaker et al., 2011]. Little is known about this type of
106 tool composite use within and across chimpanzee populations.

107 In this study, we examine tool use in army ant predation by chimpanzees at the
108 Seringbara study site in the Nimba Mountains, Guinea (West Africa). First, we
109 investigate army ant species preference by comparing chimpanzee consumption of army
110 ant species to their availability. Moreover, we examine the altitudinal distribution of
111 army ant species in relation to chimpanzee range use. Chimpanzees at Seringbara
112 inhabit mountainous terrain with the highest peak reaching 1752 m [Koops, 2011]. The
113 chimpanzees preferentially use areas above 900 m, whereas they use areas below 800 m
114 less often than expected [Koops et al., 2013]. We test whether the relative abundance of
115 prey ant species differed with regards to altitude and habitat type and whether such
116 potential differences were linked to the relative predation frequencies. Second, we
117 assess army ant-feeding tool species selectivity, as well as the effect of tool species
118 preference on tool collection distance. If certain plant species are preferred as tool
119 material, we expect the chimpanzees to invest more effort into collecting these preferred
120 species. Lastly, we investigate the use of 'tool sets' and 'composite tools' at Seringbara.
121 Preliminary findings suggested that Seringbara chimpanzees use 'digging' tools to open
122 ant nests [Humle & Matsuzawa, 2001]. We investigate this potential use of a tool set in
123 army ant predation using long-term data and compare tool types ('dip' vs. 'dig') with
124 regards to tool dimensions and strength. In addition, we examine the use of tool
125 composites in the form of 'tree perches'.

METHODS

Study Site

The Seringbara study site (N 07.37˚; W 08.28˚) is in the Nimba Mountains in southeastern Republic of Guinea, West Africa. The study site covers about 25 km^2 of steep hills and valleys 6 km from Bossou, where a community of 12 - 23 chimpanzees has been studied for over 30 years [Matsuzawa et al., 2011]. The Nimba region has been surveyed intermittently since 1992 [Matsuzawa & Yamakoshi, 1996; Shimada, 2000; Humle & Matsuzawa, 2001]. The climate is characterized by one long rainy season between February-November and a 3-month dry season (monthly rainfall <60 mm). Since 2003, researchers or field assistants have maintained a near-constant presence at the Seringbara study site. The study population remains largely unhabituated to human observers. For more information on the study site, see Koops [2011].

Data Collection

We collected data during 62 months in six study periods: 1. September 2003 - May 2004; 2. April - August & December 2006; 3. November 2007 - December 2008; 4. March 2011 - December 2011; 5. January - December 2012; 6. January - December 2013 (Table I). KK collected the data with the help of local field assistants and students.

We estimated army ant availability to chimpanzees by recording all army ant encounters during daily reconnaissance surveys (20 days per month) in Periods 2, 3, 5 and 6. In Period 6, army ants were collected until the end of March. For each army ant encounter, we recorded habitat type, altitude and GPS location. Habitat types recorded were: 1. Primary forest (excluding riverine forest): undisturbed forest; 2. Secondary forest: forest burned or cultivated in the past; 3. Riverine forest: forest <30 m wide, along permanent watercourse; 4. THV-dominated forest: forest with understory

151 dominated by herbaceous plants of the Marantaceae and Zingiberaceae families; 5.
152 Savannah: low- and high-altitude grasslands.

153 In addition, we noted for each ant column whether the column was: 1)
154 Migrating: emigration columns link nests and all the brood is transported on them from
155 the old to the new nest and many workers carry the colony's brood; 2) Foraging:
156 workers running in both directions and food items being transported back to the nest.
157 We sampled workers from each ant column, swarm raid and occupied nest for species
158 identification. Army ant species included both 'epigaiec' and 'intermediate' species
159 [Schöning et al., 2005]. Species with an epigaiec lifestyle form conspicuous swarm
160 raids on the ground and in the vegetation, as well as conspicuous nests with piles of
161 excavated soil. Intermediate species hunt only in the leaf litter, and their nests are less
162 conspicuous.

163 Army ant swarms can be highly branched, especially towards the front of the
164 swarm [Peters et al., 2009]. To avoid counting the same army ant colony twice, we only
165 considered foraging columns and swarm raids of the same *Dorylus* species to be
166 independent (i.e. belonging to different colonies) when the distance between them was
167 >100 m [*sensu* Peters et al., 2009]. If trails or swarm raids of the same species were
168 found within 100 m distance, we counted them only once. A three-person team walked
169 single file to survey for ants, so as to ensure detection of all ant trails and swarms. By
170 walking single file, even inconspicuous trails of intermediate species in the leaf-litter
171 should have become visible to the second or third person, due to dispersal of the ants
172 from the trail after disturbance by footsteps of the first or second person.

173 ***** Insert Table I about here*****

174 Availability of raw materials (i.e. living plants) for ant-feeding tools was
175 recorded around a subset of army ant nests exploited by chimpanzees in Periods 3, 5

and 6. We measured all potential tool sources in the NW 90° quadrant of a 5-m radius around the ant nest [*sensu* McBeath & McGrew, 1982; McGrew et al., 2007]. We recorded plant species and classified potential tool sources as twig (tree or shrub), vine, THV or other (monocot or fern).

We identified ant-feeding tool sources whenever possible by systematically searching the area surrounding exploited ant nests and by re-fitting tools to tool sources (Periods 3, 5 and 6). We measured the distance from tool sources to the ant-dipping site with a meter tape. For ant-feeding tools we recorded the following variables:

1. Plant species.

2. Plant type: tree, vine or herb.

3. Length: measured with meter tape (in cm).

4. Width at midpoint: measured with a ruler (in mm).

5. Possible tool function: dip, dig or unknown. Digging tools are heavily coated in mud particularly at end(s). Dipping wands are usually thinner, less sturdy and not coated in mud. If no clear function could be ascribed based on the above criteria, tools were classed as 'unknown'.

6. Breaking torque (Nm): calculated by multiplying the force (measured in kg) required to break a tool by the length of the lever arm (m) of the applied force. We measured the force necessary to break a tool by fixing the tool to an immobile surface at one end and bending it with a spring balance (force applied at 90° angle) until breaking. We measured the distance between breaking point and point of attachment of the spring balance (standard arm= 0.25 m). We converted kilogram meter into Newton meter (Nm) using the formula: 1 kgm = 9.81 Nm.

Breaking torque changes over time as tools dry out and become brittle. We therefore measured breaking torque only of ant-feeding tools that were <1 day old when

found. For tools >1 day old, we approximated a torque value based on fresh material from the same plant species. We calculated a breaking torque for these tools based on measured breaking torques of fresh (non-tool) wands (N=5) of the same plant species of varying widths. We interpolated the breaking torque for a tool of a certain width by using the regression equation of breaking torque and width for that plant species. Breaking torque was recorded for tools found only in Period 3.

In addition, at ant feeding sites in Periods 5 and 6, we recorded the presence or absence of composite tools in the form of so-called 'tree perches'. Tree perches were defined as bend over tree saplings or small trees at ant-feeding sites with clear marks of chimpanzee use (i.e. marks from hands and/or feet). We recorded all tree perches used, as well as the tree species of each tree perch.

For evidence of the diet of the chimpanzees, we collected fresh (<2 days old) fecal samples below nests that were recently occupied and on trails where chimpanzees were tracked. We pre-soaked fecal samples in water and sieved them with a 1-mm mesh [*sensu* McGrew et al., 2009]. We scored army ant remains as present or absent, then stored army ant heads in 95% ethanol for later identification to species.

To monitor temporal variation in fruit availability, we created two 500-m transects (N-S, E-W) on each of 4 - 8 hills, yielding a total transect length of 4 - 8 km. We established transects according to a stratified random design across the study site. We tagged and measured the DBH of all trees and vines belonging to confirmed chimpanzee food species with a DBH ≥10 cm and with the trunk midpoint within 5 m to each side of the transect line. We noted the presence of ripe and unripe fruit during the first half of each month. Fruit was scored as: 0) Fruit absent; 1) 1-25% of canopy in fruit; 2) 26-50%; 3) 51-75%; 4) 76-100%. Phenology data were collected for July 2003 – April 2004, January – December 2008 and May 2011 – December 2013.

We calculated a monthly fruit availability index (FAI) for chimpanzee food species with the following formula [*sensu* Takemoto, 2004]:

$$FAI = [\Sigma (P_i \times F_i) / \Sigma (P_i \times 4)] \times 100$$

In which FAI is the fruit availability index (%), Pi is the basal area of the tree (cm^2) and Fi is the fruiting score of the tree.

Data Analyses

We tested data for normality using a normal probability plot and a Kolmogorov-Smirnov test [Field, 2005]. All analyses were two-tailed and significance levels were set at 0.05. We performed statistical tests in IBM SPSS version 21.0. We used Spearman's rank correlations to analyze the proportion of fecal samples containing army ant remains per month in relation to rainfall and FAI. We only included months with >10 fecal samples collected for dietary analyses. We used a Chi-square test to compare the proportion of fecal samples with army ants between the wet and the dry season months (<60 mm rainfall). We used Chi-square tests and binomial tests to compare *Dorylus* species abundance versus chimpanzee consumption. We compared *Dorylus* species distribution across altitude categories and habitat types with a Chi-square test. Subsequently, we determined the altitudinal categories in which the proportions of *Dorylus* species differed from expected proportions, based on marginal totals of the different species. We inspected the adjusted residuals (adj. res.), which are approximately standard normally distributed, and controlled for multiple testing by means of the improved Bonferroni procedure [Hochberg, 1988]. We used Mann-Whitney U tests to compare altitude use between *Dorylus* species and to compare tool properties between tool types (dip and dig).

We used a discriminant function analysis [Field, 2005] to construct a predictive model of ant-feeding tool types (dip, dig, unknown) with tool properties, i.e. length, width and breaking torque, as predictors. First, we established whether or not tool properties predicted group membership (i.e. tool type). We entered all independent variables together and determined the number of underlying dimensions (i.e. functions) by assessing significance of Wilk's λ for each variate. Second, we determined which tool properties differentiated tool types by examining canonical variate correlation coefficients. Third, we assessed whether tools with unknown function clustered with 'dipping' or 'digging' tools by examining group centroids (i.e. mean variate scores) for each tool type. Finally, we cross-validated the model and determined the percentage of tools correctly assigned to tool type.

Ethics

The research adhered to guidelines as set down by the Division of Biological Anthropology, University of Cambridge, and the American Society of Primatologists' principles for the ethical treatment of nonhuman primates. The Direction Nationale de la Recherche Scientifique in Guinea permitted data collection on the Seringbara chimpanzees in the Nimba Mountains.

RESULTS

Army ant species diversity

We collected 801 army ant samples (Table II). Most samples were *D. emeryi* (35%), followed by *D. nigricans* (34%), *D. mayri* (18%), *D. burmeisteri* (8%) and *D. gribodoi* (7%). The majority of army ants (85% of samples) encountered were foraging,

whereas migration trails and nests were rare. Chimpanzees at Seringbara ate all five *Dorylus* species recorded, as do chimpanzees at several other sites (Table II).

***** Insert Table II about here*****

Army ant consumption

Temporal variation

We collected 1089 chimpanzee fecal samples, 14% (*N*=148) of which contained army ant remains. The proportion of fecal samples with army ant remains varied across study periods, ranging from 2 – 35% of samples (Table I). The monthly consumption of army ants was not correlated with monthly rainfall (Spearman rank correlation: r_s=-0.20, *N*=45, *P*=0.18, Fig. 1). Furthermore, there was no difference in the proportion of fecal samples containing army ants between the wet (12%) and the dry (16%) seasons (χ^2=2.9, df=2, *P*=0.09). In addition, army ant consumption was not correlated with the monthly availability of ripe fruit represented by FAI (Spearman rank correlation: r_s=0.34, *N*=31, *P*=0.06). In sum, chimpanzees consumed army ants across seasons, irrespective of rainfall and fruit availability.

***** Insert Fig. 1 about here*****

Army ant species

We confirmed consumption of all five *Dorylus* species at Seringbara through dietary analyses. *Dorylus nigricans* was found in 59% (*N*=61) of fecal samples with identified army ant remains (*N*=104) and was the most frequent species in the chimpanzees' diet. *D. emeryi* was found in 19% (20/104), *D. burmeisteri* in 14% (15/104), *D. mayri* in 13% (14/104) and *D. gribodoi* in 7% (7/104) of fecal samples with identified army ant remains (Fig. 2). Furthermore, 12% (12/104) of fecal samples contained more than one army ant species and the maximum number of species per fecal sample was three species. Chimpanzee consumption of *Dorylus* species did not

299 reflect abundance of army ant species based on all occurrences sampling (χ^2=28.9,
300 df=4, *P*<0.0001, Fig. 2). The chimpanzees consumed *D. emeryi* less (Binomial test:
301 *P*<0.0001) and *D. nigricans* more (Binomial test: *P*<0.0001) than expected based on
302 availability of these army ant species.

303 ***** Insert Fig. 2 about here*****

304 We assessed whether the observed differences in consumption by chimpanzees
305 compared to availability may be linked to spatial distributions of *D. emeryi* and *D.*
306 *nigricans*. The two species did not differ in abundance across habitat types (χ^2=4.7,
307 df=4, *P*=0.32). However, *D. emeryi* and *D. nigricans* differed in abundance across
308 altitude categories (χ^2=57.8, df=3, *P*<0.0001). *D. emeryi* was encountered
309 proportionately more often below 800 m (adj. res.=4.7, *P*<0.0001, Fig. 3) and *D.*
310 *nigricans* more often above 1000 m (adj. res.=7.4, *P*<0.0001, Fig. 3). Mean altitude was
311 855 ± SD 137 m (*N*=276) for *D. emeryi* and 947 ± SD 155 m (*N*=268) for *D. nigricans*,
312 which was significantly different (Mann-Whitney U test: Z=-7.0, *P*<0.0001).
313 Chimpanzees at Seringbara preferentially use areas above 900 m and avoid areas below
314 800 m [Koops et al. 2013], and thus encounter *D. nigricans* more than *D. emeryi*.

315 ***** Insert Fig. 3 about here*****

316 *Ant-feeding sites*

317 We found 46 tool-assisted ant-feeding sites, all at ant nests. For 12 sites we were
318 able to obtain ant samples, seven of which were identified as *D. mayri*, three as *D.*
319 *nigricans* and two as *D. gribodoi*. It thus remains to be seen if chimpanzees at
320 Seringbara use tools to harvest army ants at trails.

321

322 **Tool use in army ant predation**

323 *Plant species*

We collected 221 ant-feeding tools at 46 sites, ranging from 1 to 15 tools per site (mean=4.9 ± SD 3.1 tools/site). The Seringbara chimpanzees made tools from at least 51 plant species belonging to 28 families, including trees, shrubs, vines and herbs (Table III). The most used species (43% tools) was *Alchornea hirtella*, a small tree or shrub. For 11 tools, we could not identify the plant species.

***** Insert Table III about here*****

Raw material availability and tool selection

On average, 31 potential tool sources were available per 90º NW quadrant at ant nests (*N*=22, range: 14-104). The mean number of *A. hirtella* tool sources, the most frequently-used species, was 5 per quadrant (*N*=22, range: 0-19) and these comprised 15% (98/675) of available tool sources. The proportion of tools made from *A. hirtella* plants was significantly higher than expected based on the proportion of *A. hirtella* tool sources around ant nests (χ^2=139.8, df=1, *P*<0.0001; Table III). If *A. hirtella* was available at an ant-feeding site, it almost always was used as a tool source (15/16 cases). Conversely, in 6 out of 7 cases when *A. hirtella* was not used as a tool, *A. hirtella* also was not available as a tool source in the vicinity of the ant-feeding site. In other words, chimpanzees preferred to use *A. hirtella* for their ant dipping tools (Table III).

The mean distance from the nest at which tools were collected was 2.7 ± SD 2.3 m (*N*=119, range: 0-12 m). The tool collection distance did not differ between *A. hirtella* and other tool species (Mann-Whitney U test: N_1=45, N_2=74, Z=0.066, *P*=0.95). However, *A. hirtella* differed from other plant species in the distribution across collection distance categories (χ^2=9.3, df=2, *P*=0.01, Fig. 4). Tools made of *A. hirtella* were collected significantly more often at >8 m distance compared to all other plant species combined (adj. res.=2.4, *P*=0.016, Fig. 4). In sum, *A. hirtella* tools were used

348 preferentially and chimpanzees collected these tool materials more often at a greater
349 distance from the ant nest than tool materials of other plant species.

350 ***** Insert Fig. 4 about here*****

351 *Tool properties and tool types*

352 The mean tool length was 64.2 ± SD 24.0 cm (*N*=191, range: 25.0-190 cm) and
353 mean tool width was 6.7 ± SD 2.1 mm (*N*=191, range: 3.0–14.0). Tools collected in
354 Periods 3–6 were assigned upon collection to possible tool function: Dip (*N*=112), Dig
355 (*N*=26) or Unknown (*N*=22). 'Digging' tools were found at 10 ant-dipping sites and at 9
356 of these they co-occurred with one or more dipping tools (Fig. 5). Tool length did not
357 differ between 'dipping' and 'digging' tools (mean 'dip'=60.2 ± SD 24.3 cm, mean
358 'dig'=70.0 ± SD 27.4 cm; Mann-Whitney U test: Z=1.67, *P*=0.094). However, tool
359 width differed significantly between tool types (mean 'dip'= 6.2 mm ± SD 1.7 mm,
360 mean 'dig'= 7.4 ± 2.8 SD mm; Mann-Whitney U test: Z=2.15, *P*=0.032).

361 ***** Insert Fig. 5 about here*****

362 To assess whether category of tool could be predicted statistically based on tool
363 characteristics, we performed a discriminant function analysis (DFA) with tool length,
364 width and breaking torque as predictors (Period 3 only, *N*=27 tools). The mean breaking
365 torque was 3.5 ± SD 3.4 Nm (*N*=27, range: 0.10-14.71 Nm). Of the two discriminant
366 functions calculated, the first accounted for 83% of the variance in tool characteristics
367 and the second for 17%. The χ^2 for the two functions combined equaled 20.8 (df=6,
368 *P*=0.002). The second function alone was not significant (χ^2=4.5, df=2, *P*=0.11). For
369 Function 1, the highest canonical correlation found was with tool width (0.874),
370 followed by tool torque (0.590) and tool length (0.033). This indicates that tool width
371 and torque were most important in differentiating between tool types. The distribution
372 of discriminant scores along discriminant Function 1 shows that dipping tools are

differentiated from 'digging' tools and tools with unknown function and that 'unknown' tools cluster together with 'digging' tools (Fig. 6).

***** Insert Fig. 6 about here*****

In a cross-validated analysis, Function 1 correctly assigned 78% of tools (21/27) to tool type, which is well above the level expected by chance. Dipping tools were assigned correctly more often (94%) than 'digging' (40%) and unknown tools (60%). In sum, these preliminary results show that ant-feeding tools seemingly fall into two groups based on tool width and torque. Thus, differences in tool form suggest a possible difference in tool function.

Composite tools

Seringbara chimpanzees used composite tools (i.e. ant predation tools together with a tree perch) at 40% (10/25) of army ant predation sites in 2012-2013 (while at two sites presence/absence of tree perch was not recorded). Chimpanzees used 1-3 tree perches per site. A single tree perch was used at six sites, two perches at two sites, and three perches at two sites. A total of 11 tree species were used as tree perch: *Rinoria oblongifolia* (*N*=4), *Chidlowia sanguinea* (*N*=3), *Neostenanthera gabonensis* (*N*=2), *Alchornea hirtella* (*N*=1), *Chrysophyllum giganteum* (*N*=1), *Drypetes afzelii* (*N*=1), *Manilkara obovata* (*N*=1), *Pouteria altissima* (*N*=1), *Terminalia ivorensis* (*N*=1), *Tetracera potatoria* (*N*=1) and *Xylopia parviflora* (*N*=1).

DISCUSSION

Chimpanzees at Seringbara ate all army ant species present. Originally, the chimpanzees were reported to prey on only two out of five species, *Dorylus nigricans* and *D. emeryi* [Schöning et al., 2008a], but this was due to limited sampling. Army ant

398 species availability, measured as ant species encounter rates, did not predict
399 consumption by chimpanzees. The abundant species, *D. emeryi*, was eaten less often
400 than expected, whereas the similarly abundant species *D. nigricans* was consumed more
401 often. However, when the altitudinal distribution of army ant species was taken into
402 account, army ant availability could explain chimpanzee consumption patterns. *D.*
403 *emeryi* was most abundant below 800 m, whereas *D. nigricans* occurred mostly above
404 1000 m. Given that Seringbara chimpanzees preferentially used areas above 900 m
405 [Koops et al., 2013], the ants' spatial distribution and thus chimpanzee encounter
406 probabilities with *Dorylus* species seemingly influenced the likelihood of ant predation.
407 However, further studies are necessary to test whether or not altitudinal overlap fully
408 explains the relatively high consumption rates of *D. nigricans*.

409 We estimated the relative availability of army ant prey species to chimpanzees
410 as relative encounter rates during reconnaissance surveys. Whether encounter rates
411 reliably reflect availability as perceived by chimpanzees is difficult to determine as the
412 cues chimpanzees use to detect army ant prey are unclear [Pascual-Garrido et al., 2013]
413 and as we currently do not know whether the Seringbara chimpanzees prey on army
414 ants only at nests or also at ant trails. Moreover, reconnaissance surveys have
415 shortcomings compared to standardized insect sampling methods, such as transects or
416 pitfall traps. However, our conclusion concerning differences in relative densities of the
417 various prey species in different altitudinal zones is well supported. This is because any
418 possible systematic error in estimating relative densities would have the same effect for
419 the data of each altitudinal zone so that our comparison yields valid results.

420 Our results suggest that no prey species is actively preferred or avoided so that
421 chimpanzee predation on army ants is largely opportunistic. At sites with habituated
422 chimpanzees researchers could examine whether chimpanzees indeed show no bias in

423 decisions to attack or not attack after detecting army ants of different species.
424 Information on the nutritional value of the different army ant species at Seringbara may
425 also prove informative and these analyses are currently underway. Army ant
426 consumption at Seringbara was not linked to rainfall or fruit availability. Similarly, at
427 Gashaka (Nigeria), consumption of army ants was the same in the wet and the dry
428 seasons [Pascual-Garrido et al., 2013]. At Seringbara, we did observe interannual
429 variation in army ant consumption (Table I), which may be due to ecological variables
430 not addressed in this study. In sum, chimpanzees fed on army ants across seasons,
431 suggesting a consistent role for army ants in the chimpanzee diet, possibly as an
432 important source of essential nutrients not available in the typical diet [McGrew, 2014;
433 Rothman et al., 2014].
434
435 ***Tool use in army ant predation***
436 Seringbara chimpanzees ate the same species of *Dorylus* as chimpanzees at
437 Bossou and Taï [Möbius et al., 2008]. At Bossou, chimpanzees use longer tools at nests
438 of the more aggressive epigaiec species than at nests of intermediate species. Mean tool
439 length at Seringbara was 64.2 cm, which falls in between tool lengths at Bossou used at
440 nests of intermediate (56.5 cm) and epigaiec (74.0 cm) army ant species [Schöning et
441 al., 2008a]. Taï chimpanzees dip only at nests of the less aggressive intermediate
442 species and thus use shorter tools (23.9 cm; Schöning et al., 2008a). So far, we have
443 confirmed tools only at nests of two epigaiec (*D. mayri, D. nigricans*) and one
444 intermediate species (*D. gribodoi*). Army ants often abandon their nests in response to a
445 chimpanzee attack, rendering it difficult to obtain ant samples from exploited nests for
446 identification. More extensive sampling is required to assess differences in tool lengths
447 used for the different *Dorylus* species at Seringbara.

448 Seringbara chimpanzees used at least 51 plant species as raw material for tool
449 manufacture, but showed a strong bias towards one particular woody species, *Alchornea*
450 *hirtella*. Although *A. hirtella* was a common species in the study area, it was used more
451 than expected based on availability. Other plant species may represent preferred tool
452 material, too, but we could not test this due to the low use frequencies and the low
453 availabilities. At Gashaka, chimpanzees used only 11 plant species for tool
454 manufacture, but plant species availability and tool selectivity was not assessed
455 [Pascual-Garrido et al., 2012]. At Seringbara, chimpanzees collected tool materials from
456 *A. hirtella* more often at a greater distance from the ant nest (>8 m), which further
457 suggests preferential use. Tool availability would ideally have been measured in a 12 m-
458 radius area around nests, but we fixed the 5-m sampling distance at the start of data
459 collection before knowing that chimpanzees go up to 12 m away to select suitable tools.
460 Tool species selectivity in army ant predation has so far only been reported for dipping
461 tools at Goualougo, where chimpanzees seem to prefer species of Marantaceae [Sanz et
462 al., 2010]. In addition, tool-material selectivity has been found in termite-fishing, both
463 in the Congo basin [Suzuki et al., 1995; Sanz & Morgan, 2007] and in Senegal
464 [McBeath & McGrew, 1982]. At Seringbara, preferential use of *A. hirtella* may be
465 linked to specific characteristics of this small shrub, such as abundant straight and rigid
466 branches available close to the ground. Further research in which relative toughness and
467 straightness of all available plants is measured is required to reveal the exact basis of
468 material selectivity, which in turn may shed light on the cognitive abilities of wild
469 chimpanzees.

470 We investigated the use of tool sets at Seringbara. Previous research suggested
471 the possible use of digging sticks to open army ant nests for dipping at Seringbara
472 [Humle & Matsuzawa, 2001]. Our results showed that dipping and digging tools

differed in width, but not in length. In addition, tool types differed in terms of a functional property, namely tool strength. Furthermore, we showed that tool type could be predicted statistically based on tool characteristics (i.e. width, strength), and tools with unknown function clustered together with digging tools. These findings suggest that ant-feeding tools fall into two categories, differing in tool width and strength, thus supporting a difference in function between tool types. Direct observation of army ant predation will be necessary to confirm the use of tool sets at Seringbara.

At nearby Bossou, only one case of digging stick use in army ant-feeding has been seen in over 30 years of research [Sugiyama, 1995]. Widespread use of a tool set in army ant predation has been reported for chimpanzees only at Goualougo [Sanz et al., 2010]. Some differences emerged between the 'digging' sticks found at Seringbara and the 'perforating' tools at Goualougo. The tools used at Goualougo to perforate ant nests were both thicker and longer than dipping tools, but no difference in length was found between tool types at Seringbara. Furthermore, Goualougo perforating tools often had attached leaves, whereas this was never found at Seringbara. Also, perforating tools were made of woody saplings and dipping tools of herb stalks at Goualougo. No distinction in tool material was found at Seringbara, where nearly all tools were manufactured from woody material. Most importantly, perforating tools at Goualougo seemed to function to entice ants to come out of the nest, while minimizing the ants' aggressive response and disturbance of the nest [Sanz et al., 2010]. In contrast, all army ant nests exploited by chimpanzees at Seringbara were partly dug out and thus heavily disturbed, including those nests with potential 'digging' tools present (Koops, personal observation). 'Digging' tools at Seringbara may serve mainly to open up the subterranean chambers in the ant nest, which may be difficult to reach by hand. At

497 Seringbara, all army ant nest cavities had a dense tangle of roots inside, which may
498 render manual digging difficult.

499 Lastly, composite tool use in army ant predation was common at Seringbara.
500 Chimpanzees constructed tree perches at 40% of the ant-feeding sites. No comparative
501 data on tree perch use is available from other chimpanzee study sites. Previous studies
502 showed that chimpanzees moved off the ground in 74% of ant-dipping episodes at
503 Gombe (Tanzania), in 64% of episodes in Bossou and in 60% of episodes in Goualougo
504 [McGrew, 1974; Humle & Matsuzawa, 2002; Sanz et al., 2010]. Seringbara
505 chimpanzees likely also used a variety of methods to position themselves above the
506 ground (e.g. tree buttresses, lianas), and the proportion of army ant-feeding episodes
507 perched above ant nests appears to be similar across sites.

508 To conclude, our findings highlight the interplay between army ant behavior and
509 chimpanzee tool use strategies. Chimpanzees fed on army ant species according to the
510 altitudinal distributions of both predator and prey. Moreover, chimpanzees were
511 selective in their choice of tool materials, and invested more effort in collection of their
512 preferred tool species. Lastly, chimpanzees used tool sets and composite tools in army
513 ant predation. To fully understand the complex predator-prey interactions between
514 chimpanzees and army ants, further comparative studies across chimpanzee study sites
515 are essential.

516

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629

630 **Figure legends**

631

632 Fig. 1. Monthly proportions of fecal samples with army ant remains in relation to
633 rainfall in 2012 - 2013. Values in brackets indicate monthly samples sizes.

634

635 Fig. 2. Proportion of fecal samples with army ant remains (*N*=104) versus ant trails
636 encountered (*N*=801) of different army ant species. * Binomial test: $P<0.05$

637

638 Fig. 3. Proportion of encounters for *D. emeryi* (*N*=276) and *D. nigricans* (*N*=267) across
639 altitude categories. * $P<0.05$

640

641 Fig. 4. Tool collection distance from army ant nests (0-12 m) for *A. hirtella* tools
642 compared to all other tool species. * $P<0.05$

643

644 Fig. 5. Ant-feeding tool set found at Seringbara with a digging stick above and two
645 dipping wands below.

646

647 Fig. 6. Distribution of discriminant scores along two functions used to predict ant-
648 feeding tool types (Eigen values: Function 1=1.034, $P=0.002$; Function 2=0.218, n.s.).
649 Black circles represent group centroids.